This is a digital copy of a book that was preserved for generations on library shelves before it was carefully scanned by Google as part of a project to make the world's books discoverable online.

It has survived long enough for the copyright to expire and the book to enter the public domain. A public domain book is one that was never subject to copyright or whose legal copyright term has expired. Whether a book is in the public domain may vary country to country. Public domain books are our gateways to the past, representing a wealth of history, culture and knowledge that's often difficult to discover.

Marks, notations and other marginalia present in the original volume will appear in this file - a reminder of this book's long journey from the publisher to a library and finally to you.

Usage guidelines

Google is proud to partner with libraries to digitize public domain materials and make them widely accessible. Public domain books belong to the public and we are merely their custodians. Nevertheless, this work is expensive, so in order to keep providing this resource, we have taken steps to prevent abuse by commercial parties, including placing technical restrictions on automated querying.

We also ask that you:

+ *Make non-commercial use of the files* We designed Google Book Search for use by individuals, and we request that you use these files for personal, non-commercial purposes.

+ *Refrain from automated querying* Do not send automated queries of any sort to Google's system: If you are conducting research on machine translation, optical character recognition or other areas where access to a large amount of text is helpful, please contact us. We encourage the use of public domain materials for these purposes and may be able to help.

+ *Maintain attribution* The Google "watermark" you see on each file is essential for informing people about this project and helping them find additional materials through Google Book Search. Please do not remove it.

+ *Keep it legal* Whatever your use, remember that you are responsible for ensuring that what you are doing is legal. Do not assume that just because we believe a book is in the public domain for users in the United States, that the work is also in the public domain for users in other countries. Whether a book is still in copyright varies from country to country, and we can't offer guidance on whether any specific use of any specific book is allowed. Please do not assume that a book's appearance in Google Book Search means it can be used in any manner anywhere in the world. Copyright infringement liability can be quite severe.

About Google Book Search

Google's mission is to organize the world's information and to make it universally accessible and useful. Google Book Search helps readers discover the world's books while helping authors and publishers reach new audiences. You can search through the full text of this book on the web at `http://books.google.com/`

QL
878
.C98

B 954,477

THE MORPHOLOGY OF THE MAMMALIAN SEMINIFEROUS TUBULE

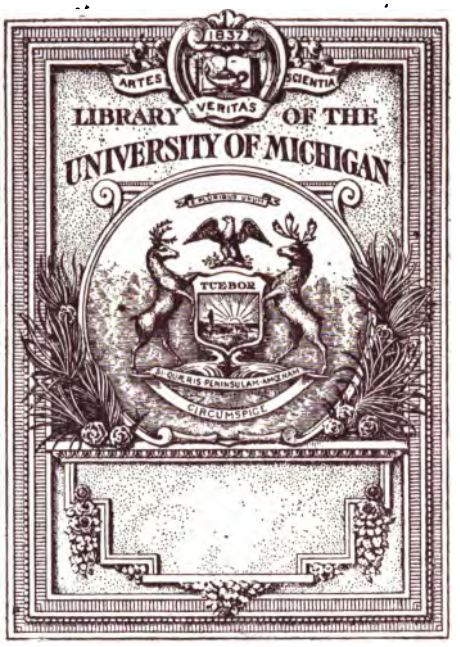
BY

GEORGE MORRIS CURTIS

Department of Anatomy, University of Michigan

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan

REPRINTED FROM
THE AMERICAN JOURNAL OF ANATOMY, VOL. 24, NO. 3,
SEPTEMBER, 1918, PHILADELPHIA


1837
ARTES
SCIENTIA
VERITAS
LIBRARY OF THE
UNIVERSITY OF MICHIGAN
TUEBOR
CIRCUMSPICE

QL
878
.C98

THE MORPHOLOGY OF THE MAMMALIAN SEMINIFEROUS TUBULE

BY

GEORGE MORRIS CURTIS

Department of Anatomy, University of Michigan

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan

REPRINTED FROM
THE AMERICAN JOURNAL OF ANATOMY, VOL. 24, NO. 3,
SEPTEMBER, 1918, PHILADELPHIA

AUTHOR'S ABSTRACT OF THIS PAPER ISSUED BY THE BIBLIOGRAPHIC SERVICE, JULY 19

Reprinted from THE AMERICAN JOURNAL OF ANATOMY, Vol. 24, No. 3, September, 1918

THE MORPHOLOGY OF THE MAMMALIAN SEMINIFEROUS TUBULE

GEORGE MORRIS CURTIS

Department of Anatomy, Vanderbilt University Medical School

TWENTY-FOUR FIGURES

CONTENTS

1. Introduction 339
2. Literature 343
   a. The seminiferous tubule 345
   b. The spermatogenic wave 342
3. Material and methods 343
4. The adult albino mouse 353
   a. The seminiferous tubule 359
   b. The spermatogenic wave 360
   c. Summary 360
5. The adult rabbit 378
   a. The seminiferous tubule 372
   b. The spermatogenic wave 373
   c. Summary 383
6. The three-week dog 388
   a. The seminiferous tubule 389
   b. Summary 389
7. Discussion 380
   a. The seminiferous tubule 381
   b. The spermatogenic wave 391
8. Summary and conclusions 392
   a. The seminiferous tubule 393
   b. The spermatogenic wave 391
9. Literature 390

1. INTRODUCTION

That there exists an interdependence of structure and function in organs is now fully recognized. In the testis, for example, the structure of the spermatogenic cells lining the seminiferous tubules indicates the functional activity of the gland in the production of spermatozoa. Consequently, in considering the morphology of the seminiferous tubule, two phases of the problem call

for consideration, one dealing mainly with the purely morphologic aspects, the other with function as expressed by structural differentiation. Under the former phase it is our purpose to consider such questions as the course, size, and relations of the tubules; under the latter, problems of spermatogenesis, particularly the functional activity of the entire tubule, as expressed in the spermatogenic wave.

The problem, as originally suggested by Dr. Huber, was essentially to isolate complete seminiferous tubules from serial sections of mammalian testes, reconstruct them, and study their form and function.

In previous work on both phases of the problem, to be considered more fully in connection with the literature, variations of the teasing method have been most commonly employed. Use has also been made of injection methods, serial sections, or, by Bremer ('11), the Born wax-plate procedure. In considering more particularly the spermatogenic function of the tubule, segments have been teased out on a slide, crushed under a coverglass, or cut into smaller pieces, oriented, and sectioned.

In this work complete serial sections have been employed as suggested above. In addition to tubules reconstructed graphically and in wax, others have been isolated by teasing, Huber and Curtis ('13). A list of the eleven tubules isolated for study has already been given by Curtis, ('15).

The portion of this paper dealing with the albino mouse seminiferous tubule was reported at the Cleveland meeting of the American Association of Anatomists, 1912–13, the teased preparations were demonstrated at Philadelphia, 1913–14, while the part dealing with spermatogenesis was presented at St. Louis, 1914–15.

2. LITERATURE

The earlier history of our knowledge concerning the structure and function of the testis has been excellently summarized by Stieda ('77). Reference should be made to this work for a critical survey of the earlier literature. The later literature is considered under two headings, in accord with the two phases of the problem.

a. The seminiferous tubule

J. Müller ('30) first described the existence of blind ends in the course of the seminiferous tubules of the squirrel. He figures a testis, with tunica albuginea removed, showing four of these structures. Apparently no critical study of these was made, and it is possible that they represent the ends of tubules broken during dissection. This is stated since the position of the blind ends is peripheral, where injury would be most likely to occur in removing the tunica albuginea. The testis figured presents no lobules, as do the dog or rabbit testes, and resembles the mouse testis in the arrangement of its tubules.

Lauth's original work ('30) I have been unable to obtain. As quoted by Mihalkovics ('73), Sappey ('89), and others, he found that the tubules originate in a peripheral 'reseau.' After teasing out fresh human tubules, he thought that if blind ends were present they were rare, as he found but one which proved to be a closed tip. Sappey ('89), who finds blind ends common, in citing this case of Lauth's thinks that more were not found because they were deep in the peripheral lobules, 1 to 3 mm. under the tunica albuginea.

Lereboullet ('51) found blind ends in the course of the rabbit seminiferous tubules. He thought that the lobules present were composed of two tubules, which united near the apex of the lobule. Lereboullet also insisted on the difference in size between tubuli contorti and tubuli recti, which was later generalized by Mihalkovics ('73) and confirmed by Stieda ('77).

Kölliker ('54) figures the tubules as ending blindly. According to Mihalkovics ('73), Beale, and Henle, whose works are inaccessible to me, found blind ends in the course of the tubules. St. George ('73), after teasing, describes and figures blind ends in the testis of a child.

Mihalkovics ('73) made studies on the testes of eleven mammals, teasing out human and dog tubules. In the human testis he describes and figures (fig. 1) a few small ampullae, .07 to .15 mm. in length, joining the tubule by a narrow neck, but finds no blind ends or side processes. In the dog he finds that the tubules form a closed network. Dichotomous branchings are present near the

apices of the lobules, the end branches of which anastomose and do not leave the lobule. He could not determine the number of tubules in a lobule. In summarizing he states (p. 252) that: "Die gewundene Samenkanälchen bilden ein Netz unter mehrfacher dichotomischer Theilung. Die aus der Theilung entstandenen Endäste hängen unter sich durch Schlingen zusammen. An den Samenkanälchen des Menschenhodens findet man in der Rindenschicht kleine knospenähnliche Ausbuchtungen der Wand."

Krause ('76) holds that the tubules present blind ends. Stieda ('77) used human and other mammalian testes, and found one or two tightly coiled tubules in each lobule. These became straight near the apices of the lobules and joined tubuli recti, one of which is described as present for each lobule. He states (p. 23) that "An der Basis des Kegels haben die einzelnen Kanälchen blinde Anfänge, Theilungen kommen vor, doch äusserst selten."

Hyrtl ('89), who used methods of injection, states that the seminiferous tubules do not end blindly as is customary for tubular glands, "sondern gehen an ihren peripherischen Enden bogenförmig in einander über."

Sappey ('89) has studied the human seminiferous tubules most thoroughly by teasing methods, using macerated and unmacerated material. He insists on the presence of blind ends and describes the occurrence of ampullae. Three forms of anastomoses were recognized: 1) From one lobule to another, as described by Lauth. These are very numerous and unite the lobules at their periphery. 2) From one tubule to another in the same lobule. These become more numerous toward the periphery of the gland, and may acquire an exceptional length. 3) From one point in a tubule to another point in the same tubule. This type forms rings, such as are shown in Bremer's ('11) and Huber's ('16) figures. Sappey thinks that in traversing the side paths afforded by these ring anastomoses, the spermatozoa would have more time to develop.

v. Ebner ('02) figures blind ends as present in the human testis. Eberth ('04), while figuring blind ends, fails to find them in teasing unstained human tubules. He corroborates Sappey in describing and figuring ampullae.

Bremer ('11) has carefully modeled a series of tubules from the testes of human embryos and fetuses ranging from 22.8 mm. to seven months of age. These are most instructive in presenting the early morphogenesis of the human seminiferous tubule. He shows that the tubules form, at first, a complete network, apparently regular in its arrangement, with blind ends at the periphery and mediastinum, and with numerous cross anastomoses forming rings. He describes a partial destruction of this network, during development, resulting in the loss of certain of the cross connections. Regarding the fate of these he states, "in the later stages, when the cords have become more established, the loose ends are not usually retracted or absorbed, but remain as short knobs or as long branches with blind ends." From his studies he concludes that, "Testis tubules may be single, ending blindly, may branch, or may anastomose."

Huber and Curtis ('13) found no blind ends in five completely teased rabbit tubules. Huber ('16) has shown that ring anastomoses are frequent in the bird testis, and points out the similarity between the bird tubules and those of a cryptorchid of the rabbit, which he teased.

b. The spermatogenic wave

The earlier history of our knowledge of spermatogenesis has been considered by Waldeyer ('06). Without going into the extensive literature of this subject, it may be well to mention some of the observations, cited by Waldeyer, which became a basis for the studies on the spermatogenic wave. Kölliker ('41–'54) showed that the wall of an active seminiferous tubule consists of several layers of cells, which differ in form and degree of development. He found the youngest cells lying along the membrana propria, the oldest lining the lumen. Sertoli ('65) recognized and differentiated the sustentacular cells. Henle ('66) described the two types of cells occurring within the tubules and pointed out the difficulty of obtaining a complete series to demonstrate the cytogenesis of the spermatozoon.

v. Ebner ('71) described eight different phases of the picture of spermatogenesis, which appeared in the various cross-sections of rat seminiferous tubules. These were readily recognized. To

ascertain the sequence of these phases along the course of the tubule, he isolated tubule-segments, 10 to 15 mm. in length, and stained them. These were mounted in clove oil or glycerin and crushed under a cover-glass. By examining the isolated cells thus obtained, he determined that the eight phases follow one another in a definite order along the tubule course. In a piece of tubule 10 to 14 mm. in length, he found from two to seven phases. Phase eight, in which the spermatozoa have just been shed, and superficial unchanged spermatids line the lumen, was found to have the briefest extent and was occasionally lacking. He found the phases variable in length, but none more than 8 mm. long. He concludes that only one phase is present in any tubule section, and states, regarding the continuity of the phases, "Es ist daher im Verlaufe ein und desselben Samenkanälchens die vollständige Reihe der Entwickelungstadien in zahlreichen Wiederholungen zu finden."

Benda ('87) studied cross and longitudinal sections of well-fixed testes of three species of mice, the guinea-pig, rabbit, bull, ram, boar, dog, and cat. He concludes that the mammalian testis is continually producing spermatozoa, since successive stages of cell development are evident in both cross and longitudinal sections. In longitudinal sections he recognized the wave-like course of the spermatogenic process. In his statement, "Wir müssen uns vorstellen, dass der Beginn neuer Umwandlungsperioden im allgemeinen vielleicht unregelmässig erfolgt, aber wellenartig jedes einzelne Kanälchen durchläuft," he intimates the variability of these waves. Benda also suggests that the cause of the phenomenon may be the wave-like progression of the secretory impulse.

Fürst ('87) announced that a wave-like formation of spermatozoa occurs in the testes of two marsupials. He isolated segments of tubules, stained them, and either examined them in sections or teased out the contained cells in glycerine. He found that in these two mammals, "Die Entwickelung in den Samenkanälchen geht in einem fortlaufenden Rhythmus oder in einer Welle."

v. Ebner ('88), isolated tubule segments, up to 95 mm. in length, from the rat testis. He cut these into smaller bits, 6 to 10 mm. in length, which were then oriented and sectioned serially. From

an examination of these portions, of tubules between 60 and 95 mm. in length, he found that the waves present varied from 25 to 38 mm. in length, averaging 32 mm. Since he observed that the waves ascend from the rete testis, he concluded that the process of spermatogenesis first began in the portion of the tubule away from the rete.

Regaud ('00) regards the wave course as spiral along the tubule, since he finds that the sides of the tubule cut in cross-section vary, and also observes irregularities in the cells lining longitudinally cut tubules.

v. Ebner ('02), accepts Regaud's findings as explaining the whirlpool-like arrangement of the fully formed spermatozoa, when they line the lumen of the rat tubule in cross-section. In this general discussion of the wave, v. Ebner points out that it would require 4.76 days for it to develop its entire length, assuming the rate of cell-division as one-half hour.

3. MATERIAL AND METHODS

The material employed in this study was very kindly furnished by Dr. Huber, who prepared it. The table below will serve to show its extent and mode of preparation. The testes used were all fixed in Flemming's solution and cut at 10 microns. The serial sections were complete, as is necessary for reconstructions. The measurements of testes given were obtained from the mounted sections of the various series. The sections were stained in iron-haematoxylin.

TABLE 1

FORM	NUMBER OF SERIES	REMARKS
Adult albino mouse, functionating testis. Age not known	2 Transverse 2 Longitudinal	Four entire glands, one measuring 7.2 mm. by 4.6 mm. by 4.01 mm.
Adult rabbit, functionating testes Age not known	1 Transverse	Central portion of gland, 6.12 mm. thick, measuring 11.5 mm. by 8.2 mm.
Three-week dog, non-functionating testes	2 Transverse	Two entire glands, measuring: A. 4.0 mm. by 2.8 mm. by 2.76 mm.; B. 3.9 mm. by 3.05 mm. by 2.8 mm.

In the study of the individual series the first problem was to isolate a complete tubule. It thus became necessary to determine among the numerous, multiform, tubule sections, just which belonged to a single, continuous tubule. This was accomplished by selecting a tubulus rectus opening into the rete testis and following it continuously through the series of sections. Camera-lucida or projection-lantern drawings and accessory reconstructions, both graphic and in wax, were employed in this process.

The question at once arises as to the possibility of determining the course of the selected tubule. Examination of a section of the testis reveals the greatly varied shape of the tubule sections. Tubule sections vary also in size. In the mouse this is not entirely due to their being cut at varying angles. It has been recognized for some time that tubule sections vary in their presentation of the picture of spermatogenesis. Consequently in passing from one 10-micron section to the next, a tubule may readily be followed, since its sections change but little in shape, size and phase of spermatogenesis.

Distinct lobules are present in the rabbit and dog testes, and are apparent in the sections. Lobules are not visible in the mouse testis. When lobules are present they serve as an additional guide, since the relation of the tubule to the lobule may be considered.

In the isolation of each tubule, except one, a complete series of projection-lantern drawings was made. These were used for the reconstructions and studies on the spermatogenic wave. In the case of the single-arched tubule of the mouse, these drawings required an extra amount of time, since it was the first isolation attempted and there were no visible divisions of the tubules into lobules for guidance. As there was nothing to indicate into which portion of the testis the tubule coiled, this was first determined by following the sections up and down the series. The portion involved, including all the tubule sections, was then drawn by camera lucida. The tubule drawings were then followed continuously and designated by numbers in a manner to be described, until the tubule ran out of the field drawn. The process was then

repeated, the camera lucida being reset to correspond to previous drawings. Where the tubules were tightly coiled or where relations were complex, the microscopic study was supplemented by graphic or wax reconstructions to assure continuity. Aid was also obtained from a partial series of camera-lucida drawings, made by Dr. Huber, covering the first part of the tubule.

In this manner a complete series of camera-lucida drawings was obtained. This series presented many surrounding tubule sections not belonging to the tubule being isolated, which were used in the isolation of the second mouse tubule. With the camera-lucida drawings as a basis, a complete series of projection-lantern drawings of the first mouse tubule was made. This procedure was regarded as a partial check on the continuity of the tubule, since, as far as possible, it was made independently and compared with the camera-lucida series, after completion.

The isolation of the second mouse tubule, which presented a branching and two arches with three tubuli recti ends, will be considered in describing that tubule.

In the case of the rabbit it was thought unnecessary to make camera-lucida drawings, as in the rabbit testis distinct lobules are present. Each lobule consists of a portion of a single tubule or tubule complex (Huber and Curtis, '13). In this paper the term sublobule is used in the sense of lobule as there employed. Consequently, serial drawings were made of two lobules and their smaller sublobules, one near the rete and mediastinum, the other radiating out from the center of the rete. Two complete series of projection-lantern drawings were made, one of a single-arched tubule, the other of a portion of a tubule complex.

In the three-week dog testis, the two complete series of projection-lantern drawings were controlled by camera-lucida drawings as will be explained later.

The graphic reconstructions (figs. 5, 6, 20, and 21) were made as follows: The final series of projection-lantern drawings were spread out on tables in sequence. A tubulus rectus end was chosen and numbered 1. It was decided that a tubule segment be regarded as that portion of the tubule between two loops or marked changes in direction. Thus the capital U would present

two segments, the capital W, four. The end attached to the tubulus rectus was followed, each succeeding section being numbered 1 to correspond to segment 1. When a loop was reached the tubule drawings were retraced and numbered 2 to correspond to segment 2. In this manner each succeeding tubule segment was numbered, and all its sections numbered to correspond. Thus each projection-lantern drawing, showing many tubule-sections, presented these numbered in sequence according to the corresponding segments. It should be stated here that in these studies the loops were all followed to their ends, to determine whether they give off branches at these points.

Each projection-lantern drawing was numbered to correspond to its section in the series. Consequently, the extent of the tubule segments was evident, and they were readily plotted on 2 mm. square paper, by the ordinary methods of graphic reconstruction. The succeeding segments were numbered as plotted.

The graphic reconstructions thus present the distribution of the tubule segments in a plane perpendicular to the plane of section. Since some segments pursue a course parallel to the plane of the graphic while others form varying angles with this plane, the graphic does not show accurately the lengths of any save straight coursing segments.

Combined with the numbered projection-lantern drawings, the graphics were used in determining the phase of spermatogenesis present in any definite portion of the tubule. Thus, if it were desired to know what phase of spermatogenesis was present where segment 10 was cut by section 90, projection-lantern drawing 90 was examined and the tubule section of segment 10 found. Serial section 90 was then compared with its projection-lantern drawing, tubule section 10 was found and its phase of spermatogenesis determined.

The models (figs. 1 to 4, 17 to 19, 22 to 24) were reconstructed from the projection-lantern drawings. The mouse and rabbit drawings were of every other section, the dog drawings of every section. The mouse and rabbit drawings were made at 100 diameters, the dog drawings at 200 diameters. Two millimeter plates were consequently used. In piling the wax plates pre-

paratory to fusing them, two factors were considered in their orientation: 1) The tunica albuginea presents a nearly constant plane for guidance. 2) Some of the tubules pursue a straight course, perpendicular to the plane of the series. These were used as guides, since wax sections of such tubules should fit accurately over the underlying section. Thus the tunica albuginea was considered a fixed plane, the straight coursing tubules as fixed points.

The segments of the model were numbered to correspond with those of the projection-lantern drawings and graphic reconstructions. Consequently, by comparing model, drawings, and sections, the phase of spermatogenesis present at any point in the course of the modeled tubule could be determined. Measurements of the model were made by passing a string over the center of the tubules, the resulting lengths being divided by 100 or 200, as required. When a wave was found to begin at one point in the model and end at another, its length was readily determined.

The methods employed in the determination of the relation of the process of spermatogenesis to the entire seminiferous tubule are as follows: Through the work of v. Ebner ('71, '88), Benda ('87), Fürst ('87), and others, it is known that the process of spermatogenesis occurs as "ein Art einer Welle," along the course of the tubule. Waldeyer ('06) designated this phenomenon the 'Samenbildungswelle' or 'unda spermiogenetica,' and v. Ebner ('88, plate 17, figs. 25 to 29), has presented such a complete 'wave' in sequence. It consists of a complete series of stages in the metamorphosis of a spermatogonium into a spermatozoon. It is here considered to commence at that point in the tubule where superficial unchanged spermatids line the lumen. It continues along the course of the tubule, embracing the metamorphosis of the spermatids, which form the superficial cells, and ends at the point where the last newly-formed spermatozoa are cast off.

A series of eight successive phases of the entire wave were arbitrarily chosen. These were determined by studies of the series and by comparison with figures such as those of Brown ('85) and v. Ebner ('88). The main differential points of the eight chosen phases are as follows:

1. Four to six layers of unchanged spermatids form the superficial cells. These are round and have pale round nuclei. There may be a few black granules scattered over their surface, depending on their proximity to phase 8. Under them are two layers of primary spermatocytes with large cell bodies and nuclei in an early prophase stage. The basal layer is a single row of darkly staining spermatogonia. The sustentacular cells have slightly conical nuclei and a short extent (v. Ebner, '88, fig. 26, *c*).

2. The spermatids have begun their metamorphosis and have united with the sustentacular cells to form the spermatoblasts. They form four or five layers, are slightly elongated and have pale, oval nuclei at one side of the cell body. Occasionally one of these nuclei stains deeply as in phase 3. The two underlying layers of spermatocytes present a late prophase stage. Under them is a single layer of deeply staining spermatogonia (v. Ebner, '88, fig. 26, *d*, and fig. 5).

3. The spermatids are more elongated, their darkly-stained nuclei are at their tips. The other layers remain little changed from phase two. The chromosomes of the primary spermatocytes stain deeply (v. Ebner, '88, fig. 27, *f*, and figs. 6, 7).

4. The outline of the future sperm head, deeply stained, is now evident. Flagellae project from the metamorphosing spermatids. The spermatoblasts are clearly outlined, and they present clumped spermatids. In this phase occur both divisions of the spermatocytes, which follow one another in close succession. Owing to the division figures, this phase is most clearly defined, the nuclei being compact and deeply stained after the metakinesis stage. The single layer of spermatogonia is deeply stained and inactive (v. Ebner, '88, fig. 27, *g*, *h*, *i*, and figs. 8, 9).

5. The spermatoblasts are now formed of elongated sustentacular cells with slender, darkly-staining sperm heads at the apices of the metamorphosing spermatids. The sperm heads do not extend more than half way through the thickness of the wall. The spermatoblasts are interspaced, toward the lumen, by three or four layers of newly-formed spermatids with pale vesicular nuclei. Some show evidence of recent activity, depending on their proximity to phase 4. The single layer of spermatogonia

shows evidence of mitosis. A layer of primary spermatocytes of intermediate size between spermatogonia and spermatids is evident (v. Ebner, '88, figs. 27, *k*, and 10).

6. The metamorphosing spermatozoa, in columns, extend deeply into the spermatoblasts, even so far as the layer of spermatogonia. Their faintly-stained heads are distinctly outlined. Between the spermatoblasts are three or four layers of spermatids, with pale vesicular nuclei. The spermatogonia are in a late prophase stage and about to divide and form the cells which become primary spermatocytes. A fine mist of granules is present about the protoplasm of the metamorphosing spermatids within the spermatoblasts (v. Ebner, '88, fig. 28, *l*, *m*, and fig. 11).

7. The metamorphosing spermatozoa now occupy the inner third of the wall of the tubule, having withdrawn from the deeper position of phase 6. The fine granules of phase 6 have become larger and more irregular about their protoplasm. The spermatogonia are in a state of active division. The surface cells are composed of four layers of spermatids (v. Ebner, '88, fig. 29, *o*).

8. The newly-formed spermatozoa are now superficial, surrounded by many irregular black granules. Under them are four or five layers of unchanged spermatids. There are two layers of primary spermatocytes as in phase 7. The newly-formed cells, which grow and form primary spermatocytes, are but little larger than the spermatogonia (v. Ebner, '88, fig. 25, *a* and *l*).

Since the different phases recorded in this study were determined chiefly from the surface cells, the metamorphosing spermatids, the most important characteristics of these cells may be briefly noted for each of the eight phases:

1. Rounded, superficial spermatids, with pale round nuclei.

2. Oval, superficial spermatids, with pale, oval, eccentric nuclei.

3. Conic spermatids, with pointed, deeply-staining nuclei at their tips, and flagellae.

4. Long, narrow, conic spermatids, with distinctly outlined, deeply stained sperm heads.

5. Long, narrow, conic spermatids in tufts, the heads within the spermatoblasts, extending about half way through the tubule wall.

6. Spermatids markedly elongated and extending in columns through the wall even to the layer of spermatogonia. A fine mist of dark granules.

7. Spermatids markedly elongated, now occupying the inner third of the wall. Many large irregular granules.

8. Superficial, newly-formed spermatozoa, surrounded by many irregular black granules.

Of course, transitions between these chosen phases were observed. Consequently, at times, a study of the deep as well as the superficial cells became necessary to decide whether a given tubule section were nearer to one or another numbered phase.

The projection-lantern drawings of the sections represented by horizontal lines in figures 5, 6 and 20; and vertical lines in figure 21 were then chosen, and the phase present in each tubule section determined and inscribed in that section. In this manner observations were made along the entire tubule at definite intervals. In the mouse these intervals are .5 mm., in the rabbit, .2 mm. In the case of the double-arched mouse tubule the drawings presented in figures 7 to 14, inclusive, were used in place of the projection-lantern drawings. Preliminary studies of the phases occurring in the single-arched mouse tubule were made at even closer intervals.

Since the tubule sections and graphic reconstructions were all numbered to correspond to the successive segments, the inscription of the phases in their proper position in the graphic was readily effected. In certain cases phases are inscribed between the horizontal lines; here they were determined from intermediate sections and drawings, or in the case of the double-arched mouse tubule by following the tubule in the sections.

4. THE ADULT ALBINO MOUSE

The material employed in this study has already been listed in table 1. Two complete seminiferous tubules were isolated from one of the series of sections. The measurements of this testis have been given. Both were reconstructed graphically and one also in wax. The occurrence of the eight chosen phases of spermatogenesis along each tubule was determined. The methods followed have been described in the previous section.

a. The seminiferous tubule

The first tubule isolated is essentially a simple, many-looped arch, with both ends attached, through tubuli recti, to the rete testis. It is presented as modeled in figures 1, 2, 3, and 4, and

Fig. 1 Model—Single-arched seminiferous tubule of the adult albino mouse, from above. The tubuli recti ends are designated A and B. End A is wired to an adjoining loop. × 33¼.

in graphic reconstruction in figure 5. The four figures of the model require little description in presenting its form. The model is a large, basket-shaped structure, measuring 33 cm. by 32 cm. by 26 cm. in depth. The cavity of the basket is presented

in figures 1 and 4, the base by figure 3, and the right side by figure 2.

The two tubuli recti ends, designated A and B (figs. 1, 2, and 4), are in close proximity at the rete. The tubule ends straighten before tapering down to join the narrower tubuli recti. End A of the model, is attached by a supporting wire to an adjacent loop

Fig. 2 Model—Single-arched seminiferous tubule of the adult albino mouse, from the rete side. End B is closely applied to the tunica albuginea, end A radiates out into the testis substance. × 33⅓.

in figure 1. Figure 4 presents it clearly defined. End A was chosen in commencing the isolation of the tubule and the connected segments and loops were the first followed. Both tubuli recti ends are patent and their lumen is continuous, through tubuli recti, with the open rete testis. A passageway for spermatozoa is thus afforded at both ends of the tubule.

The coiling is not so compact near the ends as in the opposite peripheral portion of the tubule (figs. 2 and 4). Here an accessory wax reconstruction was made to assure continuity in following the oils. The tubule segments are comparatively long; in

Fig. 3 Model—Single-arched seminiferous tubule of the adult albino mouse, from below. The rete side is at the left, the upper side of figure 1 is above. × 33⅓.

the rabbit (figs. 17, 18, 19) they are relatively shorter, owing to the greater tortuosity of the rabbit tubule.

Figure 1 demonstrates what is meant by a segment as the term is used in this paper. In the center of the figure is a prominent

U-shaped tubular portion, projecting out over the supporting wire. This consists of two segments and a loop. Each segment extends, from the loop just over the supporting wire, upward to end at another loop in the tubule course.

If this tubule were teased out it would present the form of a single arch, similar to the teased rabbit tubule shown in figure

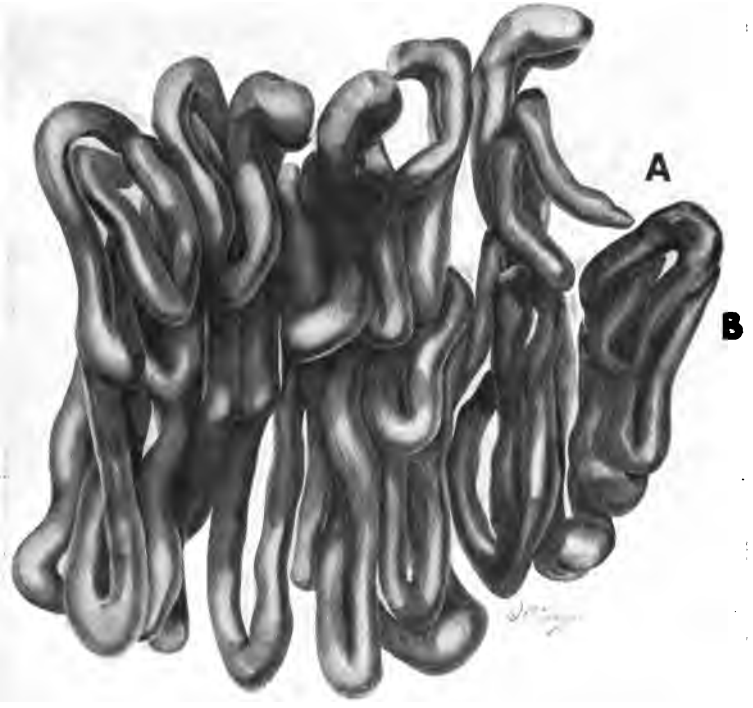


Fig. 4 Model—Single-arched seminiferous tubules of the adult albino mouse, from above. End A is clearly outlined. Drawn from a photograph. × 33⅓.

16–1. The graphic reconstruction (fig. 5) demostrates this more clearly than the model. The two tubuli recti ends are connected by over seventy segments and loops, which correspond to those of the model, end A being at the left. These tubule-segments vary in length, although no adequate idea of the length of any segment can be obtained from the graphic, owing to the varying angles of their course.

There are no indications of lobules or sublobules in the model or in the sections. Four successive regions of coiling may be arbitrarily chosen in describing the model, but these are not clearly separated.

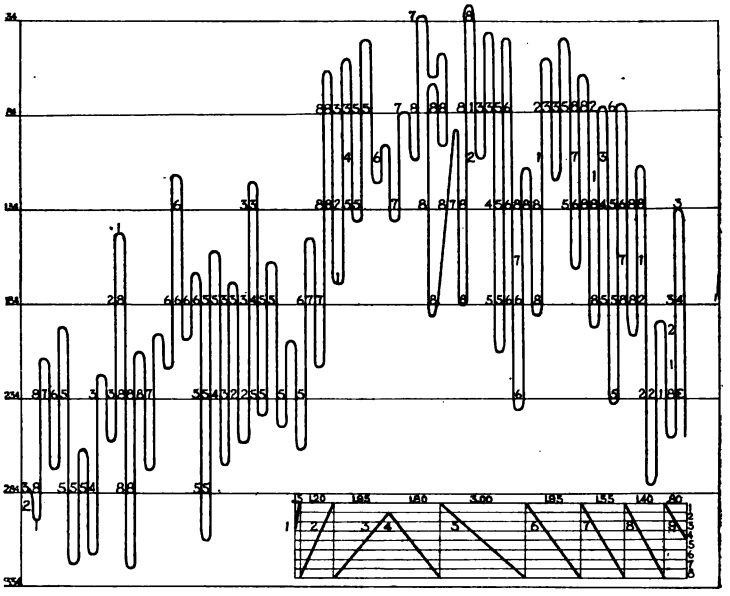


Fig. 5 Graphic reconstruction—Single-arched seminiferous tubule of the adult albino mouse, presenting the occurrence of eight chosen phases of spermatogenesis along its course. The horizontal lines represent every fiftieth section, their number in the series is placed at the left. These sections are presented in figures 7 to 13, inclusive, section 34 as fig. 7, 84 as fig. 8, etc. The numbers representing the phase of spermatogenesis present are placed at the left of the point of observation. The appended diagram represents the continuity of the phases occurring in the graphic. The actual waves are represented by heavy lines, the continuity of phases 1 and 8 by lighter vertical lines. The irregularity of wave 9 is not represented. The wave numbers are placed at their left, their lengths above, and the phases, represented by the interval between two horizontal lines of the diagram, are numbered at the right.

The second tubule is doubly arched (fig. 6). The first branching observed in the series appeared in the form of a Y, with a lumen continuous into each of the three limbs. These were numbered and followed through the series to their ends, which joined tubuli recti near the rete testis. It was thought unnecessary to

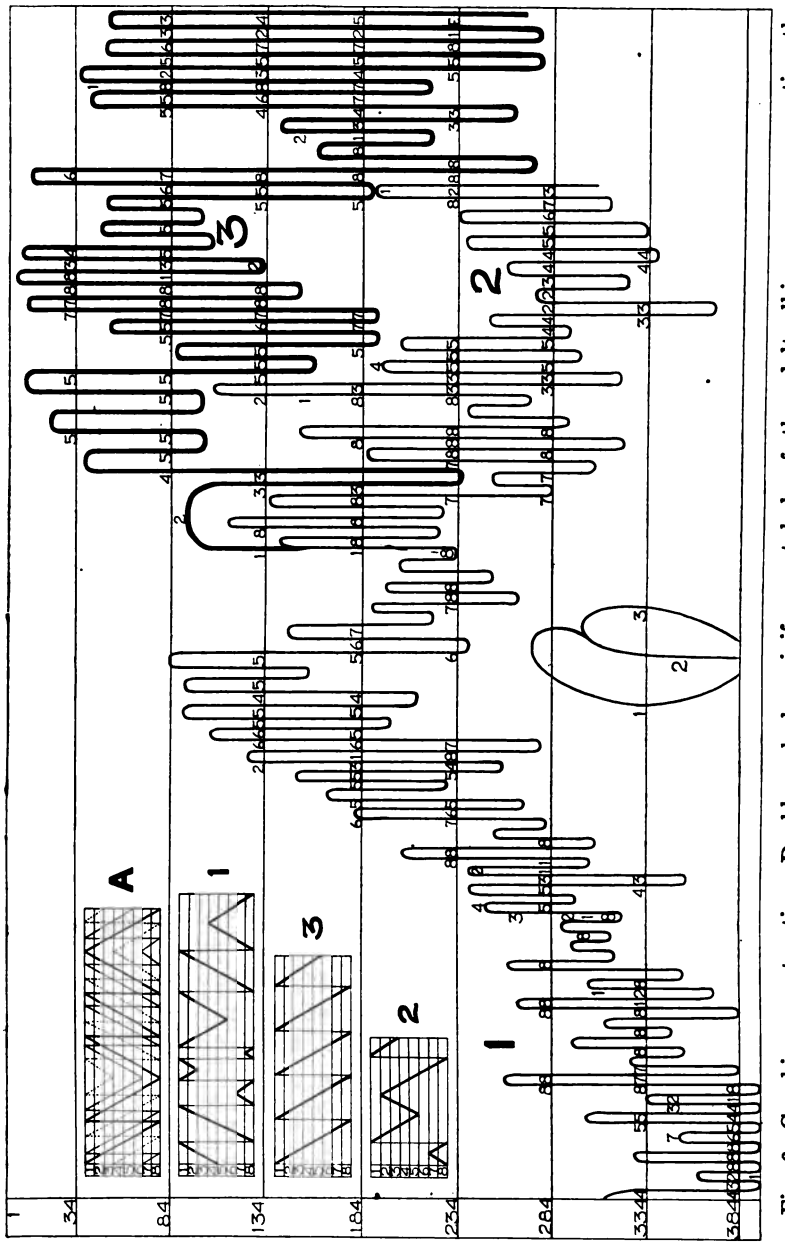


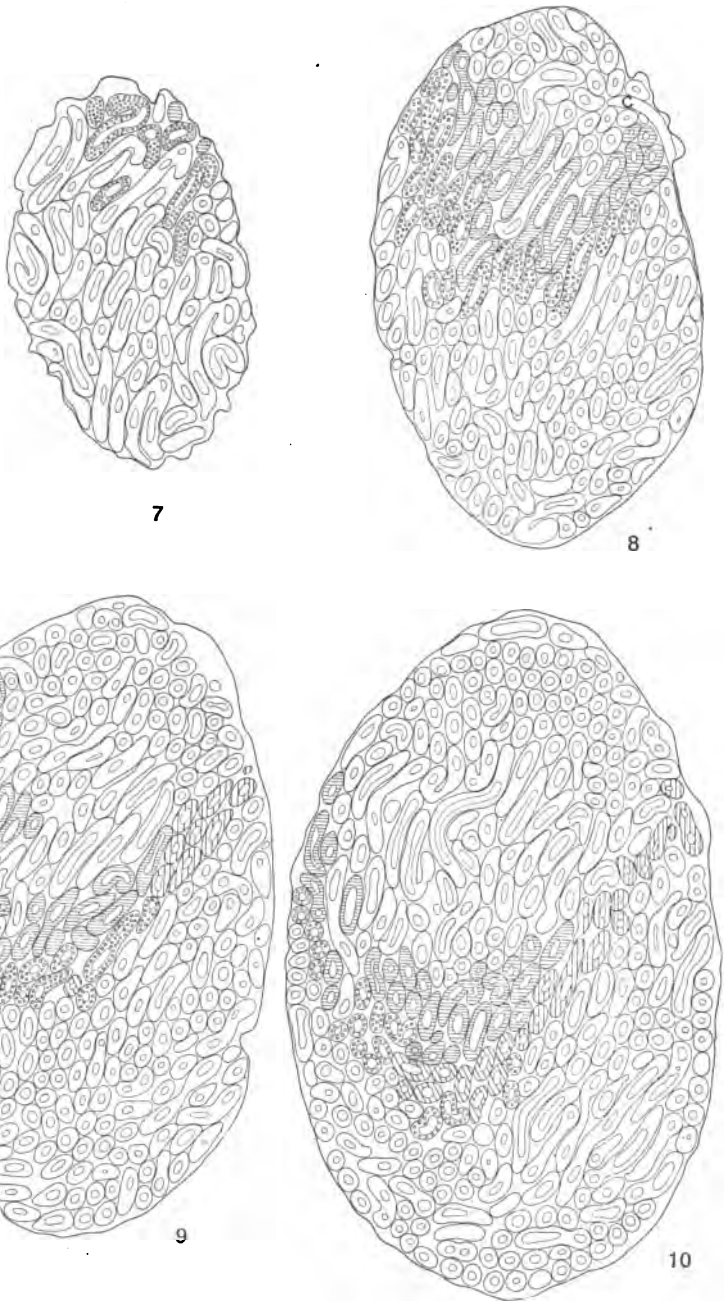
Fig. 6 Graphic reconstruction—Double-arched seminiferous tubule of the adult albino mouse, presenting the occurrence of eight chosen phases of spermatogenesis along its course. The general arrangement is the same as in figure 5. The tubule is presented schematically in the small appended diagram below. Diagrams 1, 2, and 3 present graphically the waves present in the corresponding limbs, the rete end of 1 is at the left, of 2 and 3, at the right. Diagram A indicates the schematic development of a varying series of complete waves, plotted graphically. The eight phases are numbered at the left of the diagrams.

make a complete series of drawings for this unit, as there were available the camera-lucida drawings made for the first tubule and a series of projection-lantern drawings of the entire testis (figs. 7 to 14, inclusive). The close association of the two tubules, as shown in figures 7 to 14, permitted the use of the camera-lucida drawings to a limited extent. As the tubule was followed, its segments were numbered and a graphic reconstruction (fig. 6) made. Each tubule segment appearing in section in figures 7 to 14 was in this manner numbered to correspond to its graphically reconstructed segment.

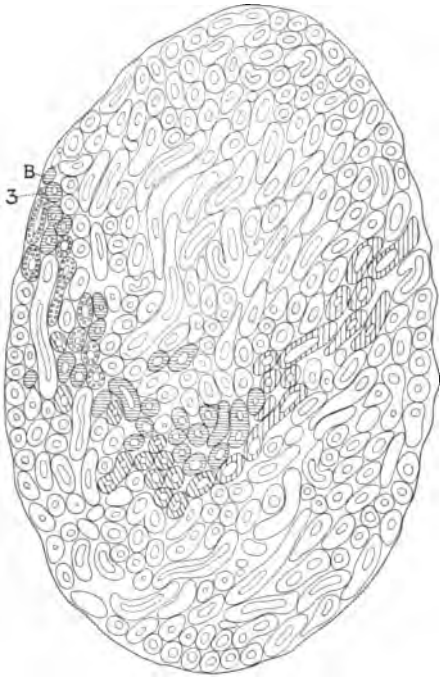
This second tubule consists of three limbs meeting at a branching. It is essentially a double arch, as shown in the appended diagram below, in figure 6. The three tubuli recti ends are patent and thus allow a passage of spermatozoa from each end into the rete, through open tubuli recti.

The distribution of both tubules in the testis is presented in figures 7 to 14, inclusive. An examination of these with the legend will indicate their relations. In the figures the most striking feature is the absence of any separation of the tubules into lobules. The modeled tubule, its sections shaded by horizontal lines, does not extend to the outer tunica albuginea. The double-arched tubule is more extensive. As indicated by its distribution in figures 7 to 14, it would form a basket-shaped model of even more pronounced depth, fitting over the convexity of the single-arched tubule.

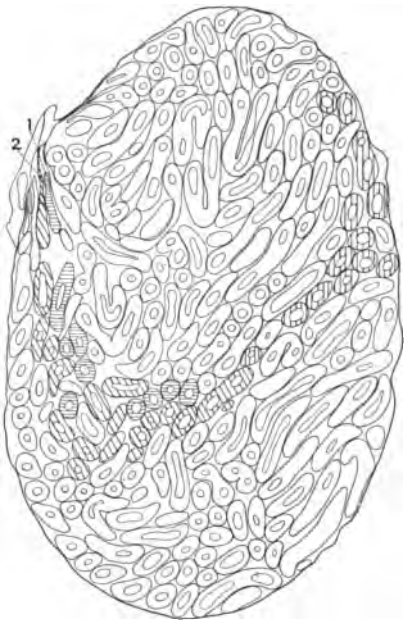
There were found to be thirty-three tubuli recti in the testis from which the two tubules were isolated. These were enumerated by making a complete series of camera-lucida drawings through the rete testis and all the adjacent tubules. Each tubulus rectus was then numbered and followed, in the drawings, into the attached convoluted tubule. The various tubules were also designated by colored crayons to avoid confusion and indicate when all the tubules had been considered. Where necessary the sections were examined microscopically, as in the case where certain tubuli recti were cut transversely and applied, slightly flattened, to the tunica albuginea. Each tubulus rectus was attached to the rete and a convoluted tubule, and all possessed a



Figs. 7 to 14 Sagittal sections—Adult albino mouse testis, representing every fiftieth section of the series, or intervals of .5 mm. The distribution and relations of the single-arched and double-arched tubules are demonstrated by differential shading. The single-arched tubule-sections are shaded by horizontal lines, limb 1 of the double-arched by vertical lines, limb 2 by oblique lines, and limb 3 by small circles. The sections correspond to the horizontal lines of figures 5 and 6. The absence of connective-tissue septa and lobules is to be noted, as well as the basket-shape of both tubules if modeled. The thin surrounding tunica albuginea

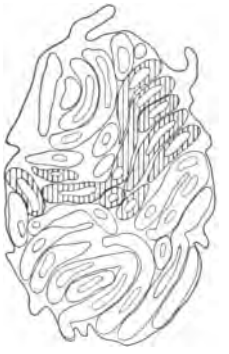


11



12

13



14

is represented by a heavy line. The blood-vessels are not drawn, except one large capsular vessel, designated C, at the upper right of figure 8. The branching of the double-arched tubule is between figures 9 and 10. Fig. 12, at the left, presents the tubulus rectus of limb 2, designated 2, passing to the rete; at the right of this is the A end of the single-arched tubule, designated 1, about to join its tubulus rectus. Fig. 11, at its upper left, presents the B end of the single-arched tubule, designated B, shown enlarged in figure 15. This joins its tubulus rectus .16 mm. on in the series. Just below it is the tubulus rectus end of limb 3, in cross-section, designated 3. × 12.5.

lumen, consequently it is thought that all are functional in allowing a passage of spermatozoa. The tubuli recti of the mouse are lined by a simple squamous epithelium.

But two branching tubules were observed in the series of the testis from which the two tubules were isolated. By assuming the presence of a third unobserved branching in the series, it is reasonable to estimate the number of tubules present as fifteen, twelve single-arched and three double-arched, since there are thirty-three tubuli recti ends. This estimate is based, of course, on the hypothesis that all the tubules are arranged in the form of arches, as are the two isolated. A third branching might possibly exist in a plane perpendicular to that of the sections, in this case it would be overlooked unless actually followed. The number has been previously estimated as sixteen, (Huber and Curtis, '13). This was before the observation of the second branching. Undoubtedly the number present is small, and there are fewer tubules in the mouse than in the rabbit, dog, or human testes which have been examined.

From measurements on the model it was found that the single-arched tubule is 13.8 cm. in actual length. The double-arched tubule is estimated as about 25 cm. in length on this basis. 1.83 cm. is regarded as an average wave length, as will be explained later. Limb 3, figure 6, judging from its number of regular waves, should be about 8.5 mm. in length. Limb 3 is apparently intermediate in length between limbs 1 and 2, considering the number of segments and loops as a guide. This roughly estimated length is nearly that of the double-arched rabbit tubule (fig. 16–3), which is 26.7 cm. in length.

Branchings are infrequent in the mouse testis, but two having been observed in repeated examinations of one series. In both a lumen was continuous into all three limbs. The second branching was only followed far enough to make certain that a short blind end was not present. If an anastomosis be regarded as the portion between two branchings in the course of a single tubule, none were found in the mouse testis.

No indications of blind ends or ampullae were observed in any examination of the mouse testis. Hence it is thought that they

are absent in the adult mouse. A slight variation in the size of the tubules was observed, which has also been noted in teased tubules of the Norway and Albino rat. These enlargements are not ampulliform, but occur regular along the tubule course, forming slight spindle-shaped enlargements. The explanation of this condition is not known.

An examination of the sections represented in figures 7 to 14 reveals no visible indication of lobules, since no connective-tissue septa divide the tubules into groups. There may possibly be lobules as regards blood supply. However, as shown by Hill ('07), there is no such lobule in the pig testis, and judging from his figures of the pig and mouse testis, which appear to have a similar blood supply, there is apparently no vascular unit in the mouse testis.

Though lobulation is not indicated, that the tubules are arranged in lobular masses, without the connective-tissue sheath, is demonstrated by the model and indicated in figures 7 to 14. From these it is evident that the individual tubule masses, as present in the mouse testis, are basket- or cup-shaped, one fitting into the concavity of the next.

b. The spermatogenic wave

The methods employed in studying the relation of the process of spermatogenesis to the two isolated tubules have been described. The results, showing the occurrence of the eight chosen phases along the course of the two complete tubules, are presented in figures 5 and 6 and their appended diagrams.

By noting the succession of phases occurring along the course of these graphically represented tubules, it is readily recognized that a definite progression of phases exists, as described by v. Ebner ('88), an "Art einer Welle." When complete and regular this wave consists of an unbroken series of phases 1 to 8, inclusive. However, the results obtained show that not all the waves are complete nor are all regular. Also they do not always follow one another in the same order.

The succession of phases in the single-arched tubule is presented in figure 5. An examination of this figure with the legend will show the variability of the waves in their course. The appended diagram presents the succession of phases occurring in the graphic, the two ends of graphic and diagram corresponding in position. The wave lengths were ascertained by measurements of the model. The tubule segments of graphic and model were numbered to correspond, as described in the previous section. Consequently, by noting the extent of a wave in the graphic, the portion of the model occupied was readily determined. In the diagram the wave lengths are drawn to scale.

Waves 1, 2, and 3 are descending, that is, they progress from higher to lower phases when followed from the tubulus rectus end A outward along the tubule course. Beginning with the junction of waves 3 and 4, numbers 4, 5, 6, 7, 8, and 9 are ascending in continuing the same direction, that is from end A toward end B. Regarding them in this light, it is readily recognized that there is a reversal of direction between 3 and 4. The waves of both tubule ends descend to this point of reversal. This rather striking fact was surmised in following the tubule, since in some portions the flagellae of the spermatozoa pointed in one direction, in other portions in the opposite.

From the point of reversal, the waves ascend toward the rete. Whether this has any effect on the course taken by the spermatozoa is not certain. The two tubule portions on either side of the point of reversal are of unequal length. The left end, A, is 3.3 cm. in length, the right end, B, is 10.5 cm.

The waves vary in length. As indicated in the diagram (fig. 5), waves 1 and 9 are incomplete, the remaining seven vary from 1.2 cm. to 3 cm. in length. The average length of the seven complete waves is 1.83 cm. This is a little more than one-half the average length, 3.2 cm., given by v. Ebner ('88) for the rat. Waves 3, 2, and 1 become progressively shorter from the point of reversal, likewise waves 5, 6, 7, 8, and 9 also diminish in length in passing toward the other end of the tubule.

The individual waves vary in their course: 1, 2, 6, 7, and 8 are in regular continuous progression, while 3, 4, 5, and 9 present

irregularities in their extent; 1 is incomplete, occurring at a tubulus rectus ending; 3 and 4 have no phase 1 in their extent. Undoubtedly they had at an earlier stage of their development, but the extent occupied by phase 2 has now developed from that formerly occupied by phase 1. This is explained later by diagram A, fig. 6. Wave 5, the longest, has two extents of phase 7 occurring out of order in phase 8. It is probable that here there is a different rate in the metamorphosis of the spermatids. Wave 9 has the following progression of phases: 4, 3, 2, 1, 8, 1, 2, 1. If plotted graphically it would present two reversals of direction, at 8 and 2, hence it is regarded as an incomplete, doubly-reversed, descending wave. The irregularity may be explained by regarding the regions out of order as developing at a varying rate.

In figure 6 is presented the occurrence of the succeeding phases of spermatogenesis along the course of the double-arched tubule. The manner of construction of this figure was essentially the same as figure 5. In making the observations of phases, use was made of the drawings (figs. 7 to 14) and their corresponding sections, together with the graphic. The occurrence of succeeding phases in sequence along these limbs is plotted in diagrams, 1, 2, and 3 of figure 6. The arrangement of these diagrams is the same as that in figure 5, except that all the waves are regarded as of average equal length, since measurements were not available.

Diagram 1 (fig. 6) presents the waves occurring along limb 1, from the rete end to the branching. Beginning at the rete end, the left, as phase 4, the first incomplete wave descends regularly through phase 1. This is followed by a complete descending wave. A marked irregularity then occurs, similar to wave 9 of figure 5. Phases 8, 7, 8, 1, 2, 1, 8, follow in order. This is also regarded as a doubly reversed descending wave; however, it is incomplete. Then occur an incomplete reversed ascending wave and a complete descending wave. The limb terminates with an incomplete reversed descending wave, ending at the branching as phase 1.

The succession of phases as waves along limb 2 (diagram 2) presents similar variable conditions. There follow from the right rete ending, an incomplete descending wave, a doubly-reversed

descending wave, and a portion of a reversed incomplete descending wave.

Limb 3 presents a striking regularity of its waves (diagram 3). From the right end, at the rete, there follow five ascending waves, the first incomplete.

Diagram A represents graphically the development of a series of varying complete waves. From the left there are indicated by heavy lines a complete ascending, a reversed ascending, a complete descending, and a reversed descending wave, in order. The broken line represents the graph of these same waves if each phase were to develop through three phases. The light line presents their graphic condition after having developed through six phases. The irregular figures, thus obtained, similar to some in the diagrams of figures 5, 6, 20, and 21, aid in the interpretation of the graphs of reversing waves presented in these figures.

The various waves, portions of waves and single phases occurring out of order in the two tubules, are arranged in tabular form in table 2. The single-arched tubule is there regarded as consisting of two limbs, meeting at the point of reversal of waves 3 and 4. The double-arched tubule consists of three limbs diverging from the branching. The wave course is considered as ex-

TABLE 2

Group 1. Complete waves, eleven, as follows:	
1. Complete unbroken descending waves	10
2. Complete descending waves, with two extents of phase 7 out of order: wave 5, fig. 5	1
3. Complete ascending waves, broken or unbroken	0
Group 2. Incomplete waves, six, as follows:	
1. Descending waves, tubuli recti endings	4
2. Descending waves, having no extent of phase 1: waves 3 and 4, fig. 5	2
3. Ascending waves	0
Group 3. Reversed waves, six, as follows:	
1. Incomplete descending waves, reversing to ascending, simple reversal: wave 3, diagram 2; wave 6, diagram 1	2
2. Incomplete ascending wave, reversing to descending, simple reversal: wave 4, diagram 1	1
3. Doubly reversed descending waves, incomplete: wave 9, fig. 5; wave 2, diagram 2; wave 3, diagram 1	3
Group 4. Single phases out of order, two, as follows:	
1. Phase 7 occurring in phase 8: wave 5, fig. 5	2

tending from the tubulus rectus ending outward along these five limbs. This table includes all the wave variations with the exception of the reversal between waves 3 and 4 in figure 5.

The general wave course may be concluded from a consideration of the above table. All eleven of the complete waves, and the six incomplete waves descend from the rete; that is, they progress from more to less developed phases as the course of the tubule is followed outward. The incomplete waves at four rete ends are descending. There are no ascending waves. Since seventeen of the twenty-three waves are wholly descending and all five tubuli recti ends are occupied by descending waves, the general wave course is regarded as descending. The three doubly-reversed waves begin and end as descending, as wave 2, diagram 2. v. Ebner ('88) finds that in the rat the waves ascend from the rete, which is opposite to the condition found in two mouse tubules.

At the right end of the single-arched tubule (fig. 5), where one of the horizontal lines (section 234) intersects the last segment, is the letter E instead of a numbered phase. The same condition is present at the right end of limb 3 (fig. 6). This signifies the presence of an embryonic condition at this point of the tubule. Here the structure resembles that of a young non-functionating tubule (fig. 15) rather than the appearance of one actively functionating. In cross-section the tubule presents no evidence of spermatogenic activity unless it be the mitotic figures in the sexual cells (*S.*, fig. 15). It differs markedly from the ordinary tubules section. Two types of cells are present, distinct, active, sexual-cells with deeply stained nuclei, and indefinite sustentacular cells (*St.*, fig. 15), apparently forming a syncytium, with pale oval nuclei and dark globular nucleoli. Strands of protoplasm nearly obliterate the lumen (*L.*, figl. 5), leaving but a small passageway for spermatozoa. This segment is closely applied to the tunica albuginea (*T. A.*, fig. 15), as also shown in figure 11, *B.*

This region of embryonic structure has been observed in all five ends of the two isolated tubules. It is indicated by E, in the two ends mentioned, since these two are cut in cross-section (*B* and 3, fig. 11). The other three ends radiate out from the rete and are consequently cut longitudinally (1 and 2, fig. 12). In

these the last observed phase of active spermatogenesis is designated. In the longitudinal sections it may be observed that the process of spermatogenesis gradually ceases. Then occurs this region of embryonic structure, followed by the flattened epithelium of the tubulus rectus.

These ends are doubtless functional in allowing a passage of spermatozoa, since there is no evidence of the accumulation of

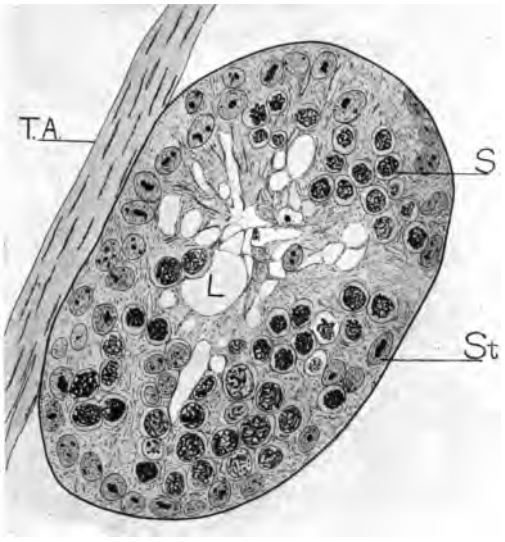


Fig. 15 Transverse section—Non-functionating tubulus rectus end of an adult albino mouse seminiferous tubule, presenting the structure of the region between the point where active spermatogenesis ceases and the tubulus rectus begins. The position of this section is shown in figure 11, B. *T. A.* tunica albuginea; *S.*, sexual cell; *st.*, sustentacular cell; *L.*, lumen. Camera lucida, × 370.

spermatozoa above them. Indeed spermatozoa have been observed in many instances within the meshes of the irregular lumen. Probably the lumen is a little shrunken in the section because of its delicate nature. Consequently, all five ends are regarded as allowing a passageway for spermatozoa. The same embryonic condition is present at the other tubuli recti ends.

This region may be a reserve for growth or regeneration. Ribbert ('90) has shown that after the removal of one testis the other undergoes a compensatory hypertrophy, the tubules increasing in volume.

c. Summary

1. Two complete seminiferous tubules were isolated from the adult albino mouse testis, and the occurrence of eight chosen phases of spermatogenesis along each determined.

2. Both tubules are arranged in the form of arches, one single, the other double, with all ends returning to the rete testis.

3. Neither tubule presented any indication of a blind end, ampulla, or blind diverticulum, nor were there any lateral anastomoses.

4. Both tubules presented regular enlargements in diameter along certain parts of their course.

5. But two branchings and thirty-three tubuli recti ends were observed in one testis, hence the number of branchings and tubules in the mouse testis is regarded as small.

6. The number of tubules in this testis is estimated as fifteen, twelve single-arched and three double-arched.

7. At each tubulus rectus end, between the points where active spermatogenesis ceases and the squamous epithelium of the tubulus rectus begins, is a region of embryonic structure. This may be a region of reserve for growth or regeneration.

8. There is no outward indication of lobules or sublobules, yet the tubules are arranged in lobular masses as shown by the two isolated.

9. The process of spermatogenesis occurs in waves along the entire course of both tubules.

10. These waves vary in length, in their individual course and in their sequence to one another. Certain of the waves present reversals of their general direction.

11. The average wave length of seven waves is 1.83 cm.

12. The general course of the waves is regarded as descending from the rete.

13. Isolated extents of single phases out of order in the wave course may be due to a variance in the rate of growth.

5. THE ADULT RABBIT

The material employed in this study has already been listed in table 1. Owing to the relatively large size of the rabbit testis, it was cut transversely into pieces and fixed in Flemming's solution, with which it had previously been injected. The central portion of the gland, measuring 6.12 mm. in thickness, was sectioned serially. This was large enough for the isolation of a single-arched tubule but did not include all of one of the larger tubule complexes

The methods employed in the isolation of a complete single-arched tubule and a portion of a many-arched tubule-complex have been given. The distinct lobules, with their smaller sublobules, in the rabbit testis, were a great aid in this procedure. One complete series of projection-lantern drawings was made for each tubule. From these both tubules were reconstructed graphically and a part of one also in wax. Every tenth drawing was used in making the observations on the spermatogenic wave.

a. The seminiferous tubule

The simpler of the two tubules, a single-arched structure, is presented in graphic reconstruction in figure 20. It consists of two tubuli recti ends, connected by over 160 short, tightly-coiled segments and loops. Both tubuli recti ends are patent and open through tubuli recti into the rete testis. If teased out the tubule would doubtless present an appearance very similar to that in figure 16–2. The horizontal lines (fig. 20), representing intervals of twenty sections or .2 mm., indicate its distribution in the series. It extends through 3.18 mm. of the testis length.

In the rabbit testis the rete is nearly central in position and surrounded by adjacent tubules except at the point where it is infolded. This tubule occupies an irregular lobule situated at the periphery of the testis, adjacent to the point of infolding for the rete and contiguous to the mediastinum. The lobule is 3.18 mm. in length, 2.5 mm. in greatest breadth, and 1.8 mm. in width. It is divided by connective-tissue septa into two smaller sublobules, one for the coils of each end. These sublobules fuse peripherally. The tubuli recti ends are relatively far apart—1.3 mm.

It appears that the portion of the testis occupied by this lobule has grown medially to surround the rete, since in two series of sections of an eight-day rabbit testis the rete is more nearly peripheral in position. The relations of the tubule give added support to this theory. If modeled the tubule would apparently form an irregular model with two bent limbs meeting in an irregular base.

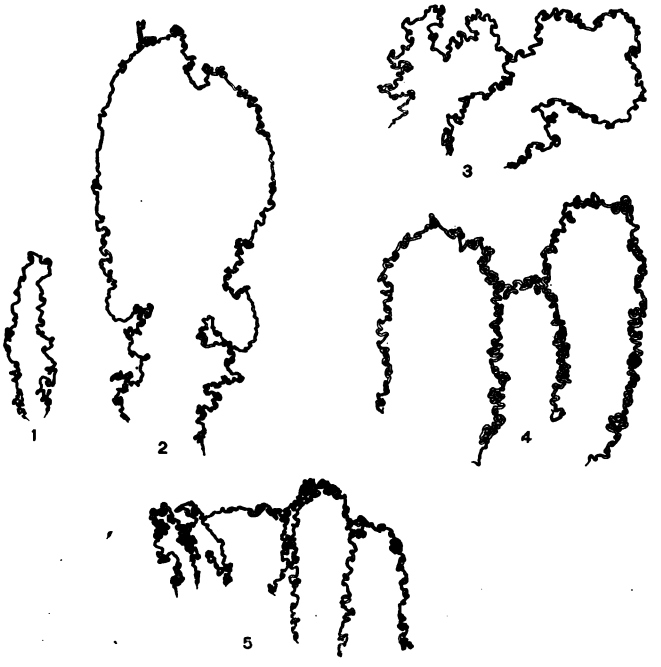


Fig. 16 Teased seminiferous tubules—Adult rabbit, actual size, presenting a series of typical mammalian seminiferous tubules isolated by Dr. Huber (Huber and Curtis, '13).

The bending would be toward the mediastinum and the flattened base would be applied to the tunica albuginea in that region. Supposedly the tubule was originally arranged in a U-shaped series of coils, which were bent toward the mediastinum during the growth of the testis.

The second tubule was not completely isolated since one of the branches extended beyond the series of sections. The isolated

portion, reconstructed graphically and in wax, is indicated by heavy lines in diagram 4, figure 21. The remainder was followed in the drawings and sections. The entire isolated portion consists of eight linked arches, with nine tubuli recti ends. These all open, through tubuli recti, into the rete testis. It is readily comparable to the six-arched tubule shown in figure 16–5. Owing to the great extent of this complex, from rete to tunica albuginea, it was not entirely reconstructed, since one regarded as essentially

Fig. 17 Model—Portion of a tubule complex of the adult rabbit testis, from the right side. The portion modeled is indicated by heavy lines in diagram 4, fig. 21. The three tubuli recti ends are designated 1, 2, and 3. The visible branchings are designated A, B, and C; the two ends of branching C are incompletely reconstructed. Drawn from a photograph. × 25.

similar had already been isolated by teasing. The only branch not followed to the rete extended beyond the series of sections.

The portion lying nearest the rete is presented in figures 17, 18, 19, and 21, which show only a part of the extended distribution. In the description of this tubule a number of terms are used, which it may be well to define. A lobule is regarded as the entire portion of the testis substance occupied by a single tubule. These lobules are distinctly separated by strands of connective tissue centrally. Their separation is less distinct peripherally. They

are apparently cone- or wedge-shaped, as a rule. Sublobules are considered as coiled masses of the tubule within the lobules, enclosed by distinct connective-tissue sheaths. A branching is any division of the tubule. A limb is considered as that portion between a tubulus rectus end and the first branching, an anastomosis as the tubule portion connecting two branchings.

The three tubuli recti ends (1, 2, 3, figs. 17, 18, 19) are in close proximity. Ends 2 and 3 have a distinct straight extent before terminating, end 1 is closely applied to its terminal segment. This condition has been frequently observed in teased tubules (Huber and Curtis, '13). The tapering junction between the tubule and its tubulus rectus is evident.

Fig. 18 Model—Portion of a tubule complex of the adult rabbit testis, from below and the left. The branchings D and E present unreconstructed ends. × 25.

Three complete sublobules and a portion of a fourth are present in the model. The boundaries of these are usually prominent notches or trenches, occupied in the sections by connective tissue. The boundaries, though not always distinct in the figures of the model, may be indicated. Each sublobule is numbered according to its tubulus rectus ending.

Sublobule 1—in fig. 17, above by the upper right border, below by an imaginary line through number 1 and parallel to end 2; in fig. 18, above by an irregular notch along the line between 2 and E, below by the lower border of the figure; in fig. 19, above by a

line between 2 and E, below by the lower border, at the left by a groove between E and the prominent wire at the lower left.

Sublobule 2—in fig. 17, above by sublobule 1, below by a line between A and C; in fig. 18, above by a line between 2 and the prominent wire-bridged notch at the left border, below by a groove along the line 2 E; in fig. 19, above by the upper border, below by the line 2 E.

Sublobule 3—in fig. 17, above by sublobule 2, below by the lower right border; in fig. 18, below by sublobule 2, above by the upper border.

Sublobule 4, which is incomplete, forms the lower left corner of fig. 17, and the upper left corner of fig. 18.

Fig. 19 Model—Portion of a tubule complex of the adult rabbit testis, from above and the left. × 25.

Each sublobule consists of a varying number of the parts of the tubule. The components of each sublobule, as observed, are as follows:

Sublobule 1—limb 1.

Sublobule 2—limb 2, branchings A and E, anastomoses AE and AB (between the corresponding branchings), and a part of the unreconstructed branch of E.

Sublobule 3—limb 3, branchings B and D, anastamoses BD, BC and BA, and a part of the unreconstructed branch from D.

Sublobule 4—branching C, anastomosis BC, and a part of the two resulting branches of C. This was only partially reconstructed.

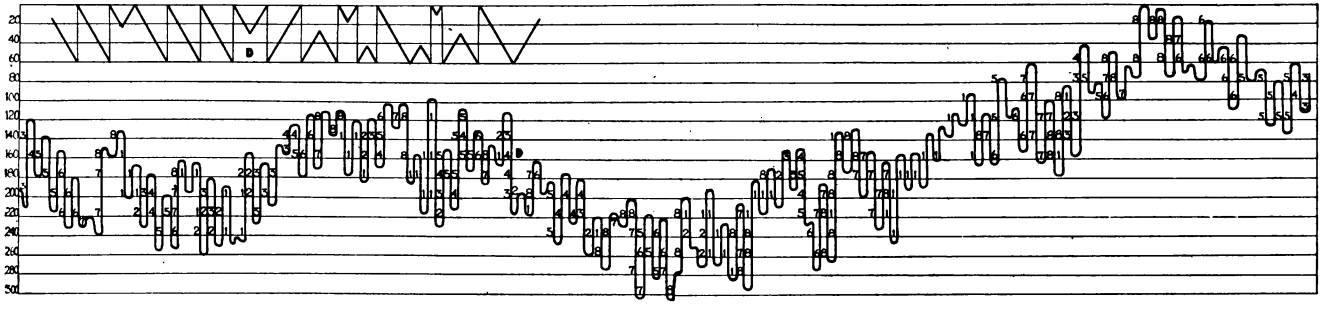


Fig. 20 Graphic reconstruction—Single-arched seminiferous tubule of the adult rabbit presenting the occurrence of eight chosen phases of spermatogenesis along its course. The general arrangement is similar to figures 5 and 6. The horizontal lines represent intervals of .2 mm., or every twentieth section. Their serial number is at the left. The diagram above presents the continuity of the phases as waves, phase 1 is above, phase 8 below. The letter D indicates the chosen point of divergence of the two limbs, as described.

It is thus evident that a sublobule may contain either: 1) a single limb only; 2) part of the three branches resulting from a branching, or 3) two branchings and part of all five resulting branches. In this tubule the branchings were found at the periphery of the sublobules. The sublobules are joined peripherally by single portions of the same tubule. It is clear from the model that a sublobule contains the parts of only one tubule.

The measurements of the lengths of adult rabbit seminiferous tubules have already been given (Huber and Curtis, '13), consequently it was thought unnecessary to measure the tubule modeled.

Five branchings are present in the portion modeled. The designation and position of these is indicated in diagram 4, figure 21, by letters. Branching A (figure 17) is formed by limb 2 in sublobule 2. After forming the tip of this sublobule, limb 2 divides as a Y, the upper of the two resulting branches forming the anastomosis AB, which occupies the upper middle portion of sublobule 2 (fig. 17), and finally emerges to branch at B. The lower forms anastamosis AE. This passes through sublobule 2, and forms the portion visible in figure 18. At E it forms the branch just above the letter.

Branching B (fig. 17) is formed by the junction of the three anastamoses AB, CB, and DB. Anastomosis AB emerges from sublobule 2 and divides, the right branch, designated by B, forms anastamosis DB which courses in sublobule 3 to branching D. The left coils in sublobule 4 and forms the upper branch at branching C (fig. 17).

Branching C (fig. 17) is a division of the anastamosis BC. The right branch, designated by C, passes to the rete in a single sublobule without further branching. The left continues outward toward the tunica albuginea, forming a new sublobule which extends beyond the series.

The position only of branching D (fig. 18) is indicated. It is formed by a division of limb 3, designated by D, which forms the tip of sublobule 3. The unreconstructed branch, visible above D, divides in its further course and forms two sublobules, each with a tubulus rectus at its tip. The anastamosis DB continues in sublobule 3, at the left (fig. 18), to branching B.

Branching E (fig. 18) is a division of limb 1, which forms sublobule 1. The upper branch EA passes into sublobule 2. The right is limb 1, the left, lettered E, forms the lower left of figure 18. Its unreconstructed end is visible above E. When followed,

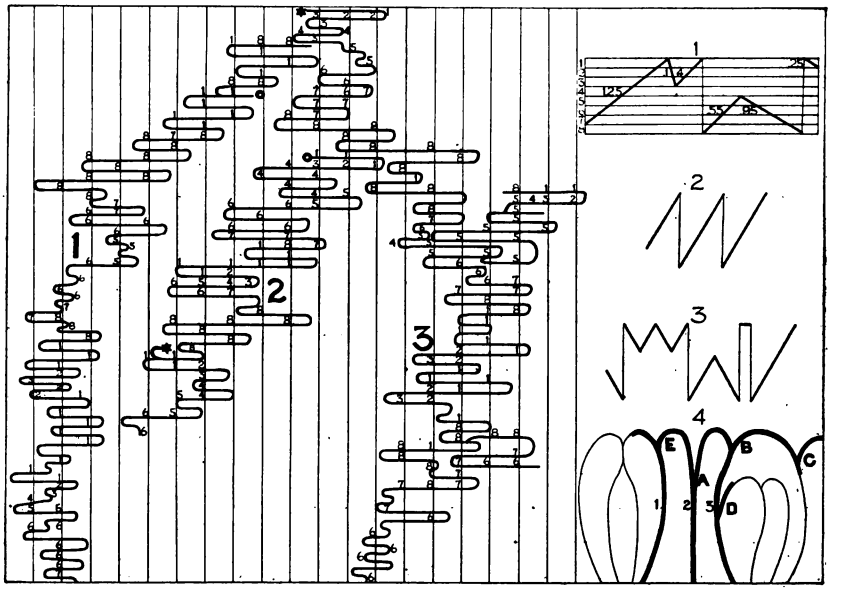


Fig. 21 Graphic reconstruction—Portion of a tubule complex of the adult rabbit testis, presenting the occurrence of eight chosen phases of spermatogenesis along its course. Diagram 4 presents the complex schematically, the portion reconstructed is indicated by heavy lines, the lighter lines representing the portion followed in the sections and drawings. Limbs 1, 2, and 3 correspond to those of the graphic and the positions of the branchings are indicated by letters. The points of broken continuity of limbs 1 and 2, are indicated by small heavy circles, of limbs 2 and 3, by stars. Diagrams 1, 2, and 3 present the phases occurring in sequence in the corresponding limbs, the rete ends being at the left, phase 1 above and phase 8 below. The waves of limb 1, are plotted to scale, their lengths are at their left.

this end was found to branch twice, the three resulting limbs all returning to the rete testis in sublobules. These branchings are all shown in figure 21.

The morphology of the adult rabbit seminiferous tubule, except the parts dealing with the relations in the testis and the

waves, has already been carefully studied by teasing methods (Huber and Curtis, '13). Since by reconstructions it has been possible to completely warrant the conclusions as given in the preliminary report, they may be reviewed briefly. In the adult rabbit the seminiferous tubules are arranged in the form of simple or linked arches, sometimes as many as twelve tubules being linked together. All the tubules return to the rete, there being no blind ends, diverticuli, or nodular enlargements in their course. An individual lobule (used in the sense of sublobule in this paper) does not indicate a complete tubule, but is to be regarded as a portion of a coil or coil complex of a single tubule in its course in the testis. Figure 16 presents a series of five tubules, teased out by Dr. Huber, as follows:

1. Short, single-arched, seminiferous tubule, similar to the mouse tubule modeled (figs. 1 to 4), and the dog tubule as presented in fig. 22. Length 9.1 cm.

2. Long, single-arched, seminiferous tubule, similar to the rabbit tubule as reconstructed in fig. 20. Length, 30.2 cm.

3. Double-arched seminiferous tubule, similar to the mouse tubule presented in fig. 6, and the modeled dog tubule of figs. 23, 24. Length 26.7 cm.

4. Three-arched seminiferous tubule, length 38.5 cm.

5. Six-arched seminiferous tubule comparable to the portion of the rabbit complex isolated (figs. 17, 18, 19 and 21). Length 30.4 cm.

This series may be regarded as a series of type forms of the mammalian seminiferous tubule, since they represent actual teased tubules similar to those found in the mouse, rabbit, and dog by reconstruction methods.

b. The spermatogenic wave

The continuity of the eight phases of spermatogenesis in the course of the two isolated rabbit tubules and the subsequent relations of the successive waves to one another were determined by the methods already described.

Figure 20, constructed in the same manner as figures 5 and 6, presents the occurrence of the phases of spermatogenesis along

the course of a single-arched seminiferous tubule of the rabbit. The diagram at the upper left of the figure is similar to the diagrams appended in figures 5 and 6. It represents the continuity of the phases as presented in the graphic below. Single phases out of order are not all represented in the diagram, but are all considered in table 3. The two rete ends of the diagram correspond in position to those of the graphic. The waves are indicated by heavy lines, the lighter lines represent the continuity of phases 1 and 8.

TABLE 3

Group 1. Complete waves, four, as follows:	
1. Complete unbroken ascending waves	3
2. Complete ascending waves, broken by having two extents of phase 4 out of order	1
3. Complete descending waves, broken or unbroken	0
Group 2. Incomplete waves, three, as follows:	
1. Incomplete ascending wave, tubulus rectus end	1
2. Incomplete ascending waves, forming together the chosen point of divergence of the two limbs of the arch	2
3. Incomplete descending waves	0
Group 3. Reversed waves, four, as follows:	
1. Reversed ascending wave, broken by an extent of phase 7 out of order	1
2. Three times reversed descending wave, becoming finally ascending, broken by an extent of phase 7 out of order	1
3. Four times reversed descending wave, becoming finally descending, broken by one extent of phase 4, three of phase 1, and one of phase 8, out of order	1
4. Doubly reversed ascending wave, unbroken	1
Group 4. Single phases out of order, nine, as follows:	
1. Phase 1 in phase 8	3
2. Phase 4 in phase 5	3
3. Phase 7 in phase 8	1
4. Phase 8 in phase 1	2

An examination of the diagram will show the continuity and variability of all the waves of the tubule. Since the variability of the waves has been described, and the irregular figures obtained by plotting the reversed waves presented in diagram A of figure 6, the diagram is self-explanatory when studied with the graphic.

From the diagram and graphic combined, the following table was obtained, the single-arched tubule being considered as con-

sisting of two limbs which diverge from the point of reversal of the incomplete reversed wave shown at the center of the diagram. The point of divergence of the limbs is indicated in the graphic and diagram, (fig. 20), by the letter D. This table presents the various waves occurring in the two limbs, their course being regarded as extending from the rete outward.

This table shows that of the eleven complete cycles and portions of cycles, four are complete ascending waves. There are no complete descending waves, and all three of the incomplete waves ascend. Furthermore, of the four reversed waves two finish as ascending waves. Thus nine out of the eleven pursue an ascending course from the rete toward the point of divergence chosen. Consequently, in this tubule, the general course of the spermatogenic wave is regarded as ascending; that is, there are to be found, in general, earlier phases at the rete end and later as one follows the tubule from the rete peripherally. This is directly opposite to the condition found in the mouse, as shown by table 1, and in accord with v. Ebner's ('88) findings in the rat.

The occurrence of phases out of order may be explained by regarding their component cells as developing at a different rate than those about them. For instance, where phase 7 occurs out of order it may be in an extent of phase 8. In phase 8 the newly formed spermatozoa are superficial, in phase 7 they are imbedded in the inner third of the tubule wall. When phases 1 and 8 occur out of order it is usually in corresponding extents of phases 8 and 1. This is doubtless due to the variability in the shedding of the spermatozoa. If at the center of an extent of phase 8 a portion of the spermatozoa were to become detached, superficial unchanged spermatids would remain and present phase 1 as occurring in an extent of phase 8.

Figure 21 presents the occurrence of the eight phases of spermatogenesis along the course of the modeled portion of the rabbit tubule complex. The relation of this portion to the remaining extent of the complex is indicated by heavy lines in diagram 4.

In this figure the limbs are not indicated as continuous. Owing to their occupation of the same region in the series, it was thought to be inadvisable to reconstruct them graphically in continuity,

hence they are broken at the circle and star. The manner of construction of this figure was otherwise as that of figure 20 and figures 5 and 6. The diagrams at the right present graphically the wave continuity, corresponding to the waves in the limbs of like numbers. The rete ends are all at the left in these diagrams and below in the large graphic. The relation of the succeeding phases of spermatogenesis to the different portions of the tubule complex may be ascertained by a combined study of the graphic and diagram.

Considering limbs 1, 2, and 3 as separate units, extending from the rete to a branching, the following table (4), was made. This indicates the relation of the wave course to the tubule course, passing outward from the rete.

TABLE 4

Group 1. Complete waves, two, as follows:
1. Complete descending waves, unbroken..... 2
2. Complete ascending waves..... 0

Group 2. Incomplete waves, two, as follows:
1. Incomplete descending wave, tubulus rectus end..... 1
2. Incomplete ascending wave, tubulus rectus end, broken by one extent of phase 8 out of order..... 1

Group 3. Reversed waves, four as follows:
1. Reversed descending wave, broken by one phase 7 out of order..... 1
2. Doubly reversed descending wave, ending as descending, broken by one phase 1 and one phase 7 out of order..... 1
3. Three times reversed ascending wave, ending as descending, broken by one phase 1 out of order..... 1
4. Three times reversed descending wave..... 1

Group 4. Single phases out of order, five, as follows:
1. Phase 1 in phase 8..... 2
2. Phase 7 in phase 8..... 1
3. Phase 8 in phase 1..... 1
4. Phase 7 in phase 6..... 1

From this table it appears that the wave course in the portion of the tubule complex modeled is very irregular and does not permit of generalization as in the other two tables. Five of the eight waves are descending from the rete in their general course. Two of the tubuli recti ends are descending and limb 2 is entirely descending. Limb 3 begins as an incomplete ascending wave. Of the reversed waves, two end as ascending and two as descend-

ing. The general course is therefore regarded as descending with some reservation. Complexity of the tubule and the junctions of the branches render this generalization more difficult. If the course be regarded as descending, as was the case in the mouse testis, the non-conformity of the single-arched tubule of the rabbit might be explained by the fact that it extends from rete toward mediastinum rather than from rete toward the peripheral tunica albuginea.

The wave length of the rabbit was not fully determined, owing to the complexity and tight coiling of the model, which made the process of accurate measurement impractical because of the inaccessibility of the tubules at its center. It was practicable to measure limb 1 entirely, owing to its superficial position. The measurements of the waves are placed at their left in diagram 1, figure 21. The incomplete wave at the rete end of limb 2 was also measured, being .55 cm. in length. The incomplete ascending wave of the rete end of limb three was found to be .8 cm. in length, while the last wave embracing all phases, shown at the right of diagram 3, was 1.4 cm. in length. This is assumed to be the average wave length after comparison with the other incomplete waves exhibited. Some idea of the variation of the length of the reversing waves may be gained by an examination of diagram 1, figure 21.

c. Summary

1. One complete and a portion of a second seminiferous tubule were isolated from the rabbit testis by reconstruction methods. The occurrence of eight chosen phases of spermatogenesis along the course of each was determined.

2. The conclusions as given by Huber and Curtis ('13, page 219) are warranted in the light of this study.

3. The two tubules are arranged in the form of arches, one single, the other composed of at least nine, with all the ends returning to the rete testis.

4. Neither tubule presented any indication of a blind end, ampulla, or blind diverticulum, nor were there any lateral anastomoses.

5. The tubules were of regular diameter along their course, and there was no indication of embryonic structure at their tubuli recti ends.

6. Branchings are frequent and usually occur at the periphery of the sublobules.

7. A lobule consists of an entire tubule surrounded by a connective-tissue sheath, the contained sublobules are definitely marked off and contain a part or parts of a single tubule in its course.

8. The lobules in that portion of the testis between the rete and mediastinum are not regularly wedge- or cone-shaped, as those radiating out from the rete to the tunica albuginea, but are distorted, presumably due to the growth of the testis around the rete.

9. The process of spermatogenesis occurs in waves along both tubules.

10. These waves vary in length, in their individual course, and in their sequence to one another. Certain of the waves present reversals in their general direction.

11. The average wave length is assumed to be 1.4 cm.

12. The general course of the wave varies considerably in extending from the rete outward.

13. The irregularity of the wave course may possibly be explained by the position of the single-arched tubule or the complexity and branchings of the larger complex.

14. Extents of single phases out of order in the waves may be due to a variance in the rate of growth.

6. THE THREE-WEEK DOG

a. The seminiferous tubule

The morphology of the non-functionating seminiferous tubule was studied in the testis of a puppy, three weeks old. Series A, already listed in table 1, was used in the isolation of two complete tubules. The immature tubules were small and tightly coiled, and since there was no lumen for guidance, extra care was necessary in determining their continuity. The desired portion of

every section was drawn by projection lantern, at a magnification of 200. These drawings were controlled by microscopic study and a complete series of camera-lucida drawings at 100 diameters. In making the first drawings, use was made of the condition, as observed in the rabbit testis, that a sublobule is composed of a portion of a single tubule or tubule complex. The distinct basement membrane was considered the boundary line where it was a question of tubule junction or contiguity. It was thought that the tubule continuity could be reasonably assured by this procedure.

Two models were reconstructed from series A, using the projection-lantern drawings. Figure 22 presents the simpler of the two, a single-arched tubule. The two narrowed tubuli recti are patent at this time and continue into the open rete, as shown by the sections. A striking difference between this and the other tubules modeled is the absence of extended coiling. Points of later growth and coiling are indicated by elevations and depressions visible in the figure. The most marked coiling is at the periphery, i.e., toward the tunica albuginea. This indicates that future growth will be largely peripheral. The figure requires little further description, save that the tubule at no point showed a fusion of its parts.

The model is 56 cm. in length, making the actual tubule 2.8 mm. in length. The tubule occupied a small, distinct, conical lobule .85 mm. in length and .35 mm. in diameter at the peripherally situated base. This extended from the rete about half way to the tunica albuginea. It may be stated here that this tubule is regarded, on the basis of these studies, as a typical tubular unit of the mammalian testis in its undeveloped form.

The second tubule reconstructed was double-arched; a single-branched tubule with all three ends connecting with the rete by tubuli recti (figs. 23 and 24). The figures, with their legends, require little further description. The three tubuli recti are open and continue into the open rete testis, as shown in the sections. The three ends are in close proximity at the rete, coiling is more pronounced peripherally, and a distinct lobule with component sub-lobules is evident. Comparison with figure 21 serves to indicate that the region of greatest growth is toward the periph-

22

23

Fig. 22 Model—Single-arched, non-functionating seminiferous tubule, from the three-week dog testis. ½ actual size.

Fig. 23 Model—Double-arched, non-functionating seminiferous tubule, from the three-week dog. The three tubuli recti ends are numbered to correspond with their limbs, 1, 2, and 3. The short limb, 1, branches at A, the lower branch returning as limb 2, the upper as limb 3. There are four sublobules present. Sublobule 4 is the prominent wedge-shaped mass above, sublobule 3 extends from its lower left border, below, to end 3. Sublobules 1 and 2 form the lower right of the figure. Sublobule 2 presents only five loop-tips at the right, below sublobule 1. ½ actual size.

Fig. 24 Model—Double-arched, non-functionating seminiferous tubule, from the three-week dog. The letter A designates the lower of the two branches or limb 2. Limb 3 begins just above at the left. The base of sublobule 4 forms the upper left border of the figure. It is separated from sublobule 1 by a prominent notch just below the upper left border. Sublobules 1 and 2 are separated by clear spaces below and the prolongation of this notch up through the left center of the figure. Sublobules 3 and 4 are separated by a deep clear notch in the upper right border. Sublobules 2 and 3 are separated by a wide notch extending down from this, just internal to the prominent segment at the extreme upper right. Sublobule 3 lies under sublobule 2. $\frac{1}{2}$ actual size.

ery. The presence of sublobules is indicated by the intertubular spaces and clefts of figure 23. These are filled by intertubular connective tissue.

The close relationship of the sublobules peripherally indicates the manner in which they are connected by parts of the same tubule. No fusion of parts of the tubule was observed in microscopic study, even in the most tightly coiled portions of the peripheral sublobules.

The tubule consists of three limbs, corresponding to the three numbered tubuli recti ends, which meet at the branching (A, fig. 23). Limb 1 is short and little coiled (figs. 23 and 24). It is 1.1 mm. in actual length. Limb 2 proceeds from the lower of the two branches of limb 1 (fig. 24, A). It coils a short distance under limb 3 (fig. 24), reaches the peripheral base of the model, turns sharply and returns to end 2. It is 7 mm. in actual length. Limb 3, the longest, is the upper of the two branches (fig. 23). It coils into the base of the model above, turns to the left and forms a wedge-shaped sublobule (fig. 23), emerges from this and returns to the rete as end 3. It is 10.7 mm. in actual length. The entire tubule is 18.8 mm. in actual length.

The tubule is relatively simple as compared to the more complex rabbit tubule partially modeled. Hence it may serve to demonstrate more clearly a point already stated (Huber and Curtis, '13) that a sublobule represents a portion of a single tubule or tubule complex. It is to be remembered that the term sublobule is used in this paper instead of the term lobule employed in the preliminary report. The entire tubule occupied a conical lobule 1.5 mm. in length and 1.9 mm. in circumference at the base. This extended from the rete to the tunica albuginea. It was bounded by prominent strands of connective tissue and was subdivided into four smaller sublobules by less prominent strands.

In recognizing these sublobules, an examination of figures 23 and 24 and their legends will necessitate little further description. Sublobule 1 is spindle-shaped. It is composed of limb 1, branching A, and the resulting first portion of limbs 2 and 3. Sublobule 2 is narrow and cone-shaped, and composed of a part of limb 2. Sublobule 3 is also narrow and spindle-shaped. It is composed of

the terminal part of limb 3. Sublobule 4 is wedge-shaped and contains the portion of limb 3 between sublobules 1 and 3.

The four sublobules are connected peripherally by a single tubule-segment so that a section between the sublobules would cut but one tubule. The branching is at the periphery and near the middle of a sublobule.

The two tubules isolated present no structures which might be interpreted as blind ends. These structures were not observed in any of the studies made in isolating the tubules. Further examinations of the sections, especially of the branches, revealed none of these structures. Of course such examinations were not so complete as those made of the two tubules isolated. From its position the doubly-arched tubule modeled is regarded as apparently representative of the larger tubules. It presented no blind ends even in its most tightly coiled peripheral portion, where they are described as most common in the human testis by Sappey ('89), and where Bremer, ('11, fig. 11, x), figures one in a seven-month human fetus. The less prominent elevations in the course of the tubules are regarded as points of growth of future loops since opposite them is usually a depression. No structures which might be considered distinct blind diverticuli or nodular enlargements were observed.

In the sections branches were frequent and were found usually at the periphery of the sublobules. In the model showing a branching, all the ends connect with the rete.

b. Summary

1. Two complete seminiferous tubules were reconstructed from the three-week dog testis.

2. Both are arranged in the form of arches, one single, the other double, with all the ends returning to the rete testis.

3. Neither presents any blind ends, blind diverticuli, or ampullae, nor were any rings present in their course.

4. Branchings are frequent in the three-week dog testis, occurring usually at the periphery of the sublobule.

5. Each lobule consists of an entire tubule. The sublobules are composed of a part or parts of a single tubule. A single sublobule may contain more than one of the resulting branches of a branching.

6. The tubuli recti ends and rete testis are open at this stage. The tubules are solid and are composed of sexual and sustentacular cells. A distinct basement membrane is present.

7. Apparently the greatest growth in length and coiling is at the peripheral portion of the tubule, toward the tunica albuginea.

7. DISCUSSION

a. The seminiferous tubule

As shown in the literature review, there exists a considerable difference of opinion concerning the presence of blind ends in the course of adult mammalian seminiferous tubules. In embryonic mammalian testes the seminiferous tubules undoubtedly present blind ends, due to their mode of origin, as shown in the work of Allen ('04) and the reconstructions of Bremer ('11). From Bremer's account of the morphogenesis of the tubules, blind ends may originate during the absorption of the complete embryonic network.

The persistence of these structures, however, in adult life, is not so certain. Bremer figures them as occurring in the testis of a seven-month human fetus. E. H. Magee, in this laboratory, has reconstructed a portion of the network of an eight-day rabbit testis and finds blind ends present in the course of the tubules. An account of this work will be published later.

Since many observers have reported blind ends, especially in teased material, it is logical to consider them as a persistence of the embryonic or fetal condition which obtains in the testis. Bremer concludes that they are present in the adult, on the basis of embryonic and fetal studies.

The work here presented, eleven isolated tubules, all argues for the absence of blind ends in the tubule course of these three forms. In this, it is in entire harmony with the work of Mihalkovics and Hyrtl and nearly so with that of Lauth, since the tubules are

thought to originate in an arched, bowed or 'reseau' coiled portion at the periphery of the gland.

In describing the blind ends, the earlier observers made use of fresh testes for teasing and did not stain the tubules, consequently it is entirely possible that they were unable to determine whether all were blind or simply broken. Since blind ends are described in that portion of the gland where the coils are most intricate, and hence most difficult to tease out, it is even probable that some of the blind ends observed were really breaks in the tubule course.

In studies on macerated material, teasing is accomplished with greater facility, yet if the tubules are not stained, it is difficult to differentiate a blind end from a tubule broken just beyond a loop. For, in this case, the membrana propria may be observed to pass over the tubule tip, and unless the tip be viewed from the side, its true condition is unrecognized. In stained preparations, where the outline is more distinct, owing to the basement membrane, Dr. Huber has found that caution is necessary to avoid this error, even when using the binocular microscope.

Mihalkovics ('73) describes the presence of small bud-like projections from the wall of human seminiferous tubules. These ampullae are also regarded as occurring frequently along the course of certain human tubules by Sappey ('89), who calls them 'caecums.' Eberth ('04) figures blind diverticuli of considerable length attached to the side of a tubule by a narrower neck. None of these structures have been observed in the mouse, rabbit, or dog. In a preparation of the human seminiferous tubule, teased out by Dr. Huber, one of the nodular enlargements is visible. It consists of a small, round knob, of lesser diameter than the tubule, connected to the tubule by a short, narrow neck, barely visible. Dr. Huber's preparation was teased from the testis of a man past middle age and hence we are inclined to favor Sappey's theory that the structures result from some morbid condition, and are not normal.

b. The spermatogenic wave

As Benda ('87) pointed out, this interesting mode of spermatogenesis results in a continued production of spermatozoa in certain mammalian testes. In the mouse and rabbit the waves oc-

cur along the entire tubule course, presenting many extents of phase 8, in which the newly formed spermatozoa are about to be shed.

v. Ebner ('88), observing that the waves ascend from the rete in the rat, concludes that the process of spermatogenesis begins in that portion of the tubule away from the rete. The finding of embryonic ends, as described, is in accord with v. Ebner's theory, since the tubulus rectus end would be the last to take up the active process of sperm formation. However, in the mouse, the general wave course is descending and in the rabbit it varies, so that this work gives a rather doubtful support to that theory.

The irregularity of the waves may be due to the manner in which the solid, inactive tubules become active, at the time of puberty, in the process of spermatogenesis. Studies are now being made on the waves of the rat, to determine whether the same conditions are present in this form.

Regaud ('00) concludes that the course of the wave within the tubule is not in a straight line along its side, but rather in the form of a spiral, winding around the tubule. The tubule sections of the mouse and rabbit testes show in many cases, especially during phase 4, that one side of the tubule is not in the same stage of activity as the other. This is not so evident in longitudinal section, since the coiling renders it difficult to make sure of an exact longitudinal section. The spermatozoa of the mouse and rabbit do not extend into the lumen in whorls as in the rat tubules figured by v. Ebner. Instead their flagellae all point in one direction. Possibly they are brushed this way by the free spermatozoa passing over them.

8. SUMMARY AND CONCLUSIONS

a. The seminiferous tubule

The following conclusions seem reasonably warranted from the observations made on eleven isolated tubules of the adult mouse, adult rabbit, and three-week dog:

1. The adult seminiferous tubules of these three forms present, in their course, no blind ends, blind diverticuli or nodular enlargements.

2. In their simpler form they are arranged in the form of an arch, the tubule beginning and ending as a tubulus rectus, each attached to the rete testis, both tubule ends being open and having a functional connection with the rete.

3. The more extensive tubular complexes may be regarded as composed of a series of linked arches, joining at Y- or T-shaped divisions of the tubules, the regions of division showing no structural peculiarity.

4. The extent of linking is very small in the mouse testis, greater in the dog testis, and greatest in the rabbit testis, where as many as twelve arches may be linked in one tubule complex.

5. There are no definitely delineated lobules in the mouse testis, though these are present as regards the arrangement of the tubules. In the rabbit and dog testis lobules are present, composed of an entire tubule surrounded by a connective-tissue sheath. These are divided into sublobules, each with a separate sheath, which contain a part or parts of the single tubule. The separation of the lobules is less distinct toward the tunica albuginea.

6. Branchings are infrequent in the mouse testis, more frequent in the dog, and most frequent in the rabbit. They occur usually at the periphery of a sublobule.

7. In the mouse testis the tubulus rectus end of the seminiferous tubule is embryonic in structure, at a certain age.

8. It appears that in the dog the development of coiling begins at the outer portion of the tubule.

b. The spermatogenic wave

From observations on the waves of four seminiferous tubules, two complete from the albino mouse, and one complete and a portion of a tubule of the rabbit, the following conclusions seem reasonably warranted:

1. The waves vary in length, in continuity, in their individual course and in the general direction of their course along the tubule.

2. The waves may reverse in their individual course and in their general direction.

3. Extents of single phases out of order are present in the wave course.

4. The average wave length in the mouse is 1.83 cm., in the rabbit 1.4 cm.

5. The general course of the waves in the mouse is descending from the rete. The general course of the waves in the rabbit is irregular.

6. At branchings the waves continue unbroken in their continuity, but not in their general course.

In conclusion I wish to express my thanks to Dr. Huber for the suggestion of this problem, for material used in its study, and for helpful suggestions during the progress of the work. I am also indebted to him for extending to me the facilities of his laboratory during the summer of 1914, when this work was completed.

9. LITERATURE CITED

ALLEN, B. M. 1903 The embryonic development of the ovary and testis of the mammalia. (Preliminary account.) Biol. Bull., vol. 5.

1904 The embryonic development of the ovary and testis of mammals. Amer. Jour. Anat., vol. 3.

BENDA, C. 1887 Untersuchungen über den Bau des funktionirenden Samenkanälchens einiger Säugethiere und Folgerungen für die Spermatogenese dieser Wirbelthierklasse. Archiv. f. Mik. Anat., Bd. 30., S. 49.

BREMER, J. L. 1911 The morphology of the tubules of the human testis and epididymis. Amer. Jour. Anat., vol. 11, no. 4.

BROWN, H. H. 1885 On spermatogenesis in the rat. Quar. Jour. Micr. Sci., vol. 25, N. S., July.

EBERTH, C. J. 1904 Die männlichen Geschlechtsorgane. K. v. Bardeleben's Handbuch d. Anat. des Menschen, Bd. 7, Zweiter Theil, Abt. 2.

EBNER, V. v. 1871 Untersuchungen über den Bau der Samenkanälchen und die Entwickelung der Spermatozoiden bei den Säugethieren und beim Menschen. Rollet's Untersuchungen aus dem Institut f. Phys. u. Histol. in Graz, S. 200. Separat, Leipzig.

1888 Zur Spermatogenese bei den Säugethieren. Archiv. f. Mik. Anat., Bd. 31.

1902 Die Geschlechtsorgane. A. Kölliker's Handbuch der Gewebelehre des Menschen. 6 Auflage, 3 Hälfte. Leipzig.

FÜRST, C. 1887 Über die Entwickelung der Samenkörperchen bei den Beutelthieren. Archiv. f. Mik. Anat., Bd. 30, S. 336.

HENLE, J. 1873 Handbuch d. system. Anatomie des Menschen. Braunschweig.

HILL, E. C. 1907 On the gross development and vascularization of the testis. Amer. Jour. Anat., vol. 6, no. 4.

1909 The vascularization of the human testis. Amer. Jour. Anat., vol. 9, p. 463.